SEASONAL AND CIRCADIAN ENERGETIC PATTERNS IN AN ARBOREAL RODENT, *THALLOMYS PAEDULCUS*, AND A BURROW-DWELLING RODENT, *AETHOMYS NAMAQUENSIS*, FROM THE KALAHARI DESERT

Barry G. Lovegrove,[1]* Gerhard Heldmaier[1] and Michael Knight[2]

[1]Department of Biology (Zoology), Philipps University, P.O. Box 1929, D-3550 Marburg, Germany and
[2]National Parks Board, Kimberly, South Africa

Abstract—1. Thermal energetic profiles as a function of the maximum range of ambient air temperatures (T_a) over which normothermia could be maintained, were measured in an arboreal rodent, *Thallomys paedulcus*, and a burrow-dwelling rodent, *Aethomys namaquensis*, during the rest- and activity-times, and in summer- (LD 16:8, 30°C) and winter-acclimated (LD 8:16, 20°C) animals.

2. Both species had minimal wet thermal conductances (C_{min}) ca 42% of expected values, and thermoneutral resting metabolic rates (TRMR) 54–64% of expected values. It is proposed that the low C_{min}s are required to maintain thermal balance at the lowest daily T_as, whereas the low TRMRs are required to avoid hyperthermia induced by high daily T_as and the low C_{min} values.

3. Burrowing behaviour did not seem to influence the selection of these low parameters *per se*, but did require large seasonal fluctuations in the endothermic temperature range—the maximum range of T_a over which the animal maintained normothermia below thermoneutrality.

4. It is suggested that a continuum may exist between the water-economy hypotheses and our endothermic temperature range hypothesis, dependent upon the refugia used, diet, water availability, and heat tolerance.

Key Word Index: Thallomys paedulcus; Aethomys namaquensis; body temperature; metabolic rate; endothermic temperature range

INTRODUCTION

Small endotherms living in warm-temperate deserts are confronted with extreme physical and ecological stresses which they have to overcome on a daily and seasonal basis. Typically, these include (a) large daily temperature fluctuations, (b) unpredictable food resources, and (c) water scarcity. Not surprisingly, desert rodents and birds display certain physiological parameters, such as low thermoneutral resting metabolic rates (TRMR), which deviate by as much as 50% from similar parameters measured in cold-temperate endotherms.

To date, the majority of these data have been measured in nocturnal desert rodents, such as desert subspecies of *Peromyscus* (McNab and Morrison, 1963), gerbils, *Gerbillus* (Haim, 1984, 1987) and *Gerbillurus* (Buffenstein, 1984), and Kangaroo rats, *Dipodomys* (McNab, 1979), which typically live in thermally-buffered burrows during the day. Without exception, these studies have shown that desert rodents consistently have lower-than-expected TRMRs (40–80% of expected) and conductances (40–60% of expected).

Thermoregulatory and water balance considerations associated with the thermal regimes of burrows have clearly dominated interpretations of these patterns. One common hypothesis is that, since convective and evaporative cooling is not as effective in burrows with high relative humidities as it is aboveground, desert burrow-dwellers need to decrease their metabolic rates to avoid hyperthermia (McNab and Morrison, 1963). Moreover, a common associated conclusion is that, TRMR can only be reduced without reducing the so-called "typical mammalian body temperature" by decreasing conductance (McNab and Morrison, 1963; Shkolnik and Schmidt-Nielsen, 1976; Buffenstein, 1984; Haim, 1984, 1987).

There seems little doubt though, that since Scholander *et al.* (1950) emphasized that TRMR is "... phylogenetically nonadaptive to external temperature conditions", the influence of the macro- and micro-climate of endotherms has tended to be underplayed in the interpretation of endotherm energetics. For instance, concerning the energetics of desert subspecies of *Peromyscus*, McNab and Morrison (1963) state that "... the decreased conductances of these mice cannot be correlated with the winter temperatures or the summer minimal temperature of their environment".

Our one contention is that energetic parameters interpreted in terms of the thermal regime of endotherms, particularly those of desert endotherms, have not received adequate consideration (see Lovegrove *et al.*, 1991). We hope to show that a consideration of what we term the endothermic temperature range (ETR)—the maximum range of T_a below

*All correspondence should be addressed to: B. G. Love-grove, Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7700, South Africa.

thermoneutrality over which normothermic body temperatures can be maintained—rather than the mean of absolute maximum and/or minimum seasonal or daily T_as, provides an excellent alternative interpretation of warm-temperate, endotherm energetics. As a comparison of the possible effect of ETR, we attempt to identify the influence of the relative reliance upon thermally-buffered refugia displayed by two nocturnal desert rodents from the southern Kalahari Desert, South Africa; one strictly arboreal, *Thallomys paedulcus* (120–140 g), and the other a typical burrow-dweller, *Aethomys namaquensis* (65 g).

Thallomys paedulcus has a wide distribution ranging from east Africa to southern Africa (De Graaff, 1981). In the southern Kalahari Desert they live in groups of *ca* 8 animals and characteristically build large nests made of sticks and thorns in the mid-sections of trees, most frequently in those of *Acacia erioloba* (De Graaff, 1978, 1981; personal observation). In mid-summer, ambient air temperatures (T_a) frequently reach 40–44°C during the afternoon hours in the Kalahari Desert (Leistner, 1967). Unlike *A. namaquensis* which retreats to a burrow during the day, *T. paedulcus* remains in its nest and only emerges at dusk (Smithers, 1983).

During winter, T_as may range from -10°C at night, to as much as 38°C during the daytime (Leistner, 1967). *T. paedulcus* therefore endure one of the largest ranges of daily and seasonal ambient temperature fluctuations known for most rodents.

To investigate the daily and seasonal physiological responses to these enormous T_a variations, we measured the oxygen consumption ($\dot{V}O_2$), CO_2 production ($\dot{V}CO_2$), abdominal temperature (T_{ab}), and the maximum noradrenaline-induced non-shivering thermogenesis (NST_{max}) of *T. paedulcus* and *A. namaquensis* as a function of the maximum range of T_as possible, in winter- and summer-acclimated animals, and during rest-time and active-time circadian phases.

MATERIALS AND METHODS

Study animals

A total of 17 *Thallomys paedulcus* and 15 *Aethomys namaquensis* were trapped in the Kalahari Gemsbok National Park, South Africa, in February 1989. They were transported by road to Cape Town for veterinary inspection and then flown to Germany in late February. The animals were maintained singularly in Plexiglass cages each supplied with sawdust and a wooden nest box. All animals were fed a staple diet of "Altromin"® rodent pellets supplemented weekly with sunflower seeds and fresh apple.

Prior to any experimentation, the animals were maintained on a 16:8 LD photoperiod at a constant room temperataure of 30°C for 3 months to simulate summer-acclimation. After completion of the summer measurements, the animals were maintained on a 8:16 LD at a room temperature of 20°C for 6 weeks before commencement of winter-acclimation measurements. We attempted to acclimate all animals to 10°C under 8:16 LD initially, but *A. namaquensis* showed rapid weight loss leading to a few mortalities.

Temperature-sensitive radio transmitters (Minimitter Model X) calibrated with a mercury thermometer (0.05°C) in a water bath, were implanted intraperitoneally under anaesthesia (ketamine i.p.) to measure T_{ab}.

Nest temperatures

Temperatures of a large nest from which all *T. paedulcus* had been previously trapped were measured for 1 week with a MS 120-02 digital datalogger and copper–constantan thermocouples during August (mid-winter), 1989. Temperatures were recorded every 30 min on the nest surface and at a depth of 30 cm inside the nest.

Protocol

For each species, $\dot{V}O_2$, $\dot{V}CO_2$ and T_{ab} were measured simultaneously in 6 animals (3 males and 3 females) in six separate respirometers, as a function of T_a. Care was taken to keep the animals under their respective photoperiods during all handling procedures and measurements. For *T. paedulcus*, the same 6 animals were used in all experiments, but for *A. namaquensis*, 2 "new" similar-sized animals were used during the winter-acclimation experiments. The animals were kept at each T_a for 1.5–2.5 h (shorter time periods for very high T_as). Not more than five different T_as were measured on any one day. About 5–10 min elapsed between experimental T_a changes.

All experiments were conducted in a 1 m³ temperature cabinet (Karl Weiss, Giessen) with a regulated accuracy <0.1°C and a potential operative range of -80°C to $+60$°C, at a r.h. = 50%. A negative-pressure flow-through system using flow-rates of 30–70 l·h⁻¹ (depending on T_a) was used. All water vapour was removed immediately downstream from each respirometer sample line using a multi-input Peltier-element gas cooler (Type ECP-1, M & C Products Analysentechnik, Ratingen).

All measuring devices, including one mass-flow meter per sample line (Type FM 360, Tylan, Eching), radio receivers, a double-channel oxygen analyser (Type S-3A, Applied Electrochemistry, Sunnyvale), and a CO_2 analyser (Type UNOR 6N, Maihak AG, Hamburg), were interfaced via a 36-channel A/D converter (Type MDP 8230/35, Mess & System Technik GmbH) with a microcomputer which also controlled relay-valves switching between sample lines every 60 s. To compensate for the baseline drift of the oxygen analyser, the $\dot{V}O_2$ of an empty respirometer was measured every 7 min, and this value was subtracted on-line from the subsequent six sample measurements.

NST capacity was measured as the maximum $\dot{V}O_2$ response (mean of the five highest consecutive $\dot{V}O_2$ values for each animal) in non-anaesthetized animals ($n = 6$) during the rest-time following injections of noradrenaline (NA). NA doses, administered s.c., were calculated from Heldmaier (1970); NA (mg·kg⁻¹) = $6.6\,M_b^{-0.458}$, where M_b is body mass (g). However, these doses were found to be too high for summer-acclimated *A. namaquensis*, so the doses were reduced to those that which produced a maximum, sustained $\dot{V}O_2$ response (60% of predicted doses).

Data analysis

The mean of the lowest three $\dot{V}O_2$ measurements and the corresponding $\dot{V}CO_2$ and T_{ab} were calculated for each animal for the last 45–60 min of each measurement interval at each T_a. Linear regressions were calculated for $\dot{V}O_2$ as a function of T_a for all T_as between what could clearly be distinguished as the thermoneutral zone (TNZ) and the cold-induced $\dot{V}O_2$ maximum, or peak metabolic rate (PMR). TRMR was calculated from all constant $\dot{V}O_2$ values which did not (a) show a hyperthermic increase response at the highest T_as, or (b) show a cold-induced increase.

The intercept of the regression line of cold-induced $\dot{V}O_2$ values and T_a with TRMR was used to calculate the lower critical limit of thermoneutrality (T_{lc}) of each animal. Minimal wet thermal conductance (C_{min}) was chosen for each animal from the lowest of all values calculated from the equation $C_{min} = RMR/(T_{ab} - T_a)$ for all T_as at which the animals were considered to be normothermic.

For each animal, the following statistics were calculated according to the procedures proposed by Lovegrove *et al.* (1991):

(a) The heat production (HP), or PMR cold limit (T_{pmr})—the T_a at which the PMR of each animal was reached.
(b) The T_b cold limit (T_{hypo})—the T_a representing the onset of a continued fall in T_{ab} below the T_{ab} at T_{lc} of each animal i.e. the T_a representing the onset of hypothermia.
(c) The HP "endothermic temperature range" (T_{hp})—the range of ambient temperature between T_{lc} and T_{pmr}, i.e. $T_{hp} = T_{lc} - T_{pmr}$.

(d) The T_b "endothermic temperature range" (T_{Tb})—the range of ambient temperature between T_{lc} and T_{hypo}, i.e. $T_{Tb} = T_{lc} - T_{hypo}$.

For each species, Tukey range tests (Zar, 1984) were used to test the significance of changes of all statistics either seasonally (winter and summer), or on a circadian basis (day and night). TRMR and C_{min} values were compared with values predicted by the rodent allometric BMR equation (Hayssen and Lacey, 1985), and the non-primate day and night C_{min} allometric equations (Aschoff, 1982), respectively.

RESULTS

All mean $\pm$ SD statistics are summarized in Table 1, whereas the significance statistics of the Tukey tests are given in Table 2. For simplicity, most results are discussed using the mean value of each statistic. Although we have elected to present all energetic data in terms of $\dot{V}O_2$ (i.e. ml $O_2 \cdot g^{-1} \cdot h^{-1}$), we present the respiratory quotients calculated from $\dot{V}CO_2/\dot{V}O_2$ in Table 3 should conversion of our data to $W \cdot g^{-1} \cdot h^{-1}$ be required. For convenience, we simply refer to the two acclimation regimes as summer and winter.

Nest temperatures

The surface temperatures of the *T. paedulcus* nest varied between an absolute maximum of 29.1°C and an absolute minimum of −4.5°C (Fig. 1), i.e. an absolute daily range of 33.6°C within the week measured. The temperature measured at a depth of

Table 1. Energetic statistics of the black-tailed tree rat, *T. paedulcus*, and the Namaqua rock mouse, *A. namaquensis*, measured during the day and night in winter-acclimated (8:16 LD, 20°C) and summer-acclimated (16:8 LD, 30°C) animals (SD in parentheses)

	T. paedulcus				*A. namaquensis*			
	Summer day	Summer night	Winter day	Winter night	Summer day	Summer night	Winter day	Winter night
Body mass (g)	124.7	124.7	142.3	138.0	66.3	64.4	62.2	63.9
	(22.6)	(27.6)	(11.9)	(13.0)	(14.6)	(10.0)	(5.9)	(5.8)
TRMR (ml $O_2 \cdot g \cdot h$)	0.549	0.816	0.608	0.663	0.790	1.126	0.978	1.121
	(0.046)	(0.152)	(0.055)	(0.054)	(0.102)	(0.157)	(0.129)	(0.148)
TRMR (% of exp.)*	54.46	80.95	63.01	68.01	63.58	89.75	77.06	89.12
T_{ab} (°C)	36.12	37.59	36.00	37.15	35.80	37.62	35.90	37.96
	(0.29)	(0.23)	(0.87)	(0.42)	(1.16)	(0.98)	(0.37)	(0.38)
C_{min} (ml/g·h·°C)†	0.0639	0.0788	0.0490	0.0511	0.1060	0.1330	0.0825	0.0934
	(0.0068)	(0.0193)	(0.0056)	(0.0090)	(0.0170)	(0.0760)	(0.0115)	(0.0208)
C_{min} (ml/g·h·°C)‡	0.0615	0.0645	0.0500	0.0516	0.0815	0.0957	0.0766	0.1068
	(0.0078)	(0.0063)	(0.0031)	(0.0035)	(0.0122)	(0.0015)	(0.0046)	(0.0218)
C_{min} (% of exp.)§	48.72	77.24	42.41	65.13	46.58	81.33	42.36	90.40
PMR (ml $O_2 \cdot g \cdot h$)	2.927	2.592	2.492	2.937	3.673	3.712	4.267	3.945
	(0.242)	(0.259)	(0.247)	(0.235)	(0.563)	(0.565)	(0.678)	(0.574)
T_{pmr} (°C)	−7.98	2.53	−11.11	−15.57	−0.42	4.60	−13.53	−1.52
	(1.64)	(1.55)	(3.25)	(4.35)	(4.43)	(3.75)	(4.75)	(4.85)
T_{hypo} (°C)	−8.31	−0.518	−6.10	−18.44	−0.32	3.78	−13.76	−0.29
	(0.85)	(5.60)	(6.6)	(3.49)	(4.11)	(3.01)	(4.23)	(4.36)
T_{lc} (°C)	30.16		27.46		26.88		26.39	
	(1.18)		(1.81)		(2.53)		(1.80)	
T_{uc} (°C)	35.69		35.89		34.39		34.49	
	(0.88)		(1.11)		(1.76)		(0.88)	
NST_{max} (ml $O_2 \cdot g \cdot h$)	1.812		2.195		2.357		2.497	
	(0.215)		(0.282)		(0.381)		(0.476)	
T_{hp} (°C)	38.14		38.57		28.43		39.92	
	(2.18)		(3.04)		(4.38)		(4.28)	
T_{Tb} (°C)	>T_{hp}		33.90		28.31		40.15	
			(6.97)		(3.66)		(3.64)	

*TRMR = $4.98 M_b^{-0.331}$ (M_b = body mass in grams); Hayssen and Lacey (1985).
†Mean of the individual slopes of the regressions of $\dot{V}O_2$ and T_a below TNZ.
‡Calculated from $C_{min} = RMR/(T_{ab} - T_a)$.
§C_{min} (day) = $1.539 M_b^{-0.517}$, C_{min} (night) = $1.022 M_b^{-0.519}$ (Aschoff, 1982).

Table 2. Statistics of significance and multiple comparison Tukey tests tested at the 95 and 99% confidence level (see Zar, 1984)

	Day vs day S vs W	Night vs night S vs W	Day vs day S vs S	Day vs night W vs W
T. paedulcus				
Body mass	NS	NS	NS	NS
TRMR	NS	$P < 0.05$	$P < 0.001$	NS
T_{ab}	NS	$P < 0.05$	$P < 0.001$	$P < 0.001$
C^{*}_{min}	$P < 0.001$	$P < 0.001$	NS	NS
PMR	$P < 0.05$	NS	NS	$P < 0.05$
T_{hypo}	NS	$P < 0.001$	$P < 0.05$	$P < 0.001$
T_{pmr}	NS	$p < 0.001$	$P < 0.001$	NS
NST_{max}	$P < 0.05$			
T_{lc}	$P < 0.05$			
T_{uc}	NS			
T_{hp}	NS			
A. namaquensis				
Body mass	NS	NS	NS	NS
TRMR	NS	NS	$P < 0.001$	NS
T_{ab}	NS	NS	$P < 0.001$	$P < 0.001$
C^{*}_{min}	NS	NS	NS	$P < 0.05$
PMR	NS	NS	NS	NS
T_{hypo}	$P < 0.001$	NS	NS	$P < 0.001$
T_{pmr}	$P < 0.001$	NS	NS	$P < 0.001$
NST_{max}	NS			
T_{lc}	NS			
T_{uc}	NS			
T_{hp}	$P < 0.001$			
T_{Tb}	$P < 0.001$			

*Calculated from $C_{min} = RMR/(T_{ab} - T_a)$.
S — Summer; W — Winter; NS = not significant $(P > 0.05)$.

Body mass and oxygen consumption

30 cm inside the nest varied from an absolute maximum of 26.2°C to an absolute minimum of 0.6°C (Fig. 1), i.e. an absolute daily range of 25.6°C. On average, the maximum and minimum daily deep-nest temperatures were 2.67 ± 0.46°C cooler, and 6.26 ± 2.21°C warmer, than the maximum and minimum daily surface temperatures, respectively. Moreover, the deep-nest temperatures showed a phase delay response of 3–4 h to changes of the surface temperature of the nest (Fig. 1).

Body mass and oxygen consumption

The body mass of T. paedulcus was not significantly different between summer and winter, despite a mean increase of 14% in winter. A. namaquensis body masses also remained constant between winter and summer.

In T. paedulcus TRMR was not significantly different in the day between summer and winter (Fig. 2). These TRMR values remained constantly low at 54.5 and 63.0% of expected values. However, in summer animals, the night TRMR was significantly 26.5% higher than during the day (Fig. 3), but this was not

the case in winter animals (Fig. 4). NST_{max} was significantly 21.1% higher during winter compared with summer.

Although in A. namaquensis TRMR was 23.8% higher during the day in winter compared with summer (Fig. 5), this difference was not significant. The TRMRs in winter and summer were 63.58 and 77.06% of predicted values, respectively. However, as with T. paedulcus, the summer night TRMR was significantly higher than that in the day (Fig. 6). Unlike T. paedulcus however, there was no significant difference between the summer and winter NST_{max} values.

In T. paedulcus, the day PMR was significantly higher in summer animals, $5.33 \times$ TRMR, compared with winter animals, $4.10 \times$ TRMR (Fig. 2). However, there was no significant difference between the night PMR of summer and winter animals. In winter animals, PMR was significantly higher ($4.43 \times$ night-TRMR, $4.83 \times$ day-TRMR) at night compared with the day (Fig. 4).

In A. namaquensis the winter PMR was 16.2% higher than that in summer in the day (Fig. 5), but

Table 3. Mean respiratory quotients (RQ) for various ambient temperature intervals

|	Summer day RQ	SE	Summer night RQ	SE	Winter day RQ	SE	Winter night RQ	SE
T. paedulcus								
>30 C	0.846	0.035	0.862	0.042	0.843	0.050	0.781	0.010
20–30 C	0.845	0.046	0.784	0.021	0.894	0.040	0.781	0.016
10–20 C	0.817	0.063	0.767	0.032	0.863	0.047	0.777	0.005
−10–10 C	0.789	0.018	0.765	0.076	0.832	0.002	0.799	0.024
< −10 C					0.794	0.001	0.791	0.023
A. namaquensis								
>30 C	0.868	0.016	0.800	0.016	0.800	0.039	0.814	0.018
20–30 C	0.815	0.002	0.786	0.012	0.850	0.007	0.807	0.021
10–20 C	0.807	0.013	0.811	0.003	0.836	0.031	0.799	0.012
−10–10 C	0.817	0.025	0.786	0.005	0.808	0.001	0.787	0.020
< −10 C			0.780	0.002	0.787	0.015	0.750	0.000
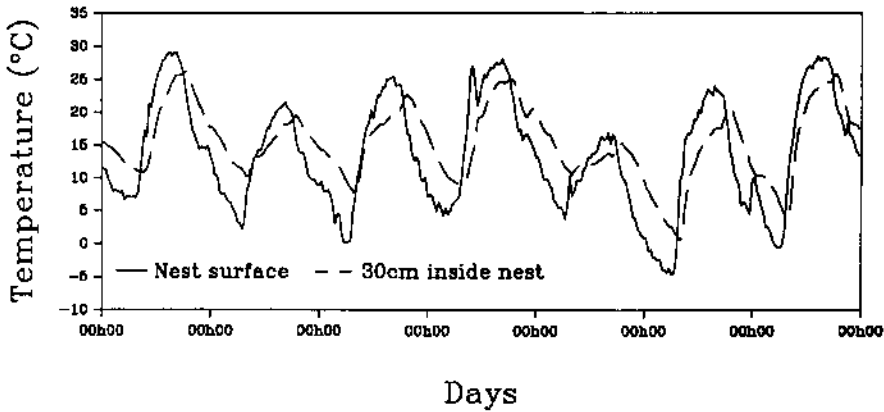
Fig. 1. Seven day recordings of temperatures of a *T. paedulcus* nest measured during mid-winter in an *Acacia erioloba* tree in the Kalahari Gemsbok National Park, South Africa, on the surface of the nest (———) and at a depth of 30 cm inside the nest (-----).

this was not significantly different from any other PMR measured.

Thermoneutral limits

During the day, the lower critical thermoneutral limit of *T. paedulcus* occurred at 30.16°C in summer, significantly higher than $T_{lc} = 27.46°C$ during winter (Fig. 2). In all animals the increase in $\dot{V}O_2$ below T_{lc} was linear during the day (Figs 2, 3 and 4), but at night this was not always the case—in some cases $\dot{V}O_2$ showed a more curvilinear increase below T_{lc} (e.g. Fig. 3), making a calculation of the winter and summer night T_{lc} unrealistic.

During the day, the upper critical thermoneutral limit of *T. paedulcus* was not significantly different between summer, 35.69°C, and winter, 35.89°C

(Fig. 2). The night T_{uc} statistics could also not be calculated because there was no clear increase in $\dot{V}O_2$ at the higher T_as within the TNZ (Figs 3 and 4).

A. namaquensis did not change T_{lc} (26.88 and 26.39°C) and T_{uc} (34.39 and 34.49°C) between winter and summer, respectively (Fig. 5). $\dot{V}O_2$ increased linearly below T_{lc} in all animals during the day, but again, this $\dot{V}O_2$ was often more curvilinear during the night (Figs 5, 6 and 7).

Metabolic cold limits

In *T. paedulcus* there was no significant difference in the T_a at which PMR was reached i.e. T_{pmr}, during the day in summer, −7.98°C, and winter, −11.11°C (Fig. 2), but there was a large difference between the night T_{pmr}s during summer, 2.53°C, and winter,
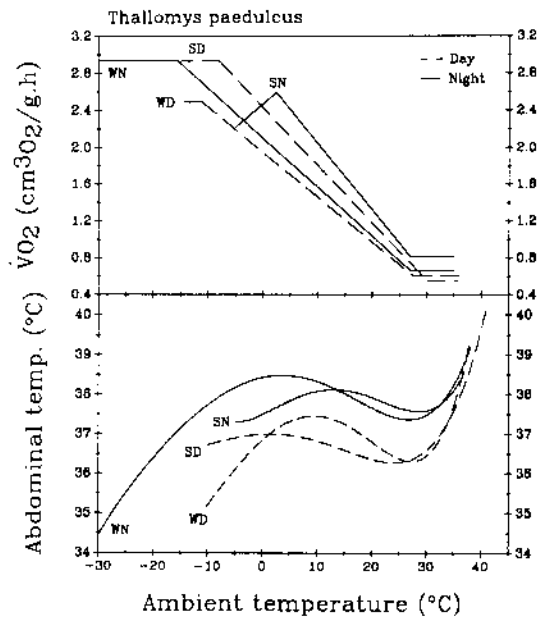

Fig. 2. $\dot{V}O_2$ and T_{ab} curves of *T. paedulcus* showing circadian and seasonal changes. The $\dot{V}O_2$ curves were drawn from the statistics given in Table 1—the actual data are given in Figs 3 and 4. The T_{ab} curves are the same as the eye-fitted curves fitted to the actual data in Figs 3 and 4. SD—summer day; SN—summer night; WD—winter day; WN—winter night.
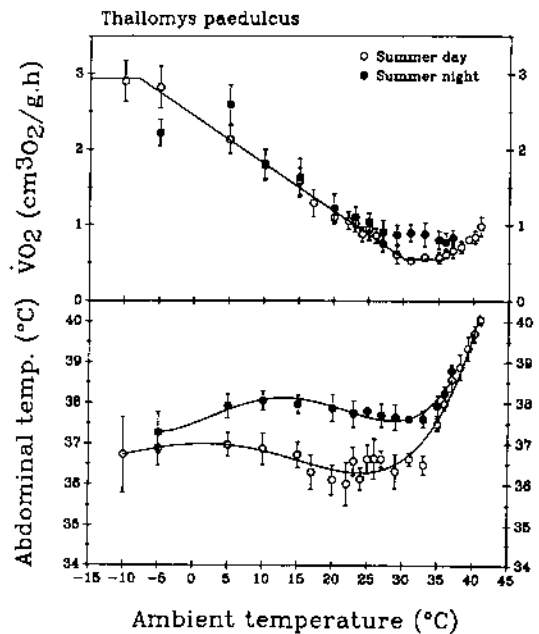

Fig. 3. Mean ± SD $\dot{V}O_2$ and T_{ab} of summer-acclimated *T. paedulcus* during the day (○) and night (●). The T_{ab} curves in this figure, and all equivalent subsequent figures, were eye-fitted for graphic clarity.
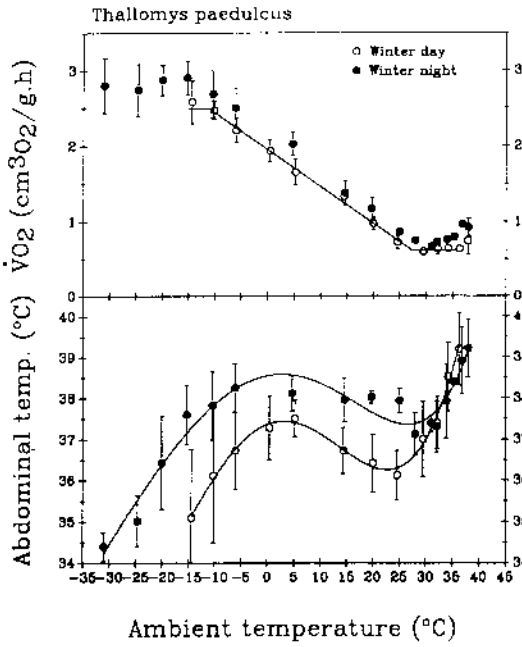
Fig. 4. Mean ± SD $\dot{V}O_2$ and T_{ab} of winter-acclimated *T. paedulcus* during the day (O) and night (●).
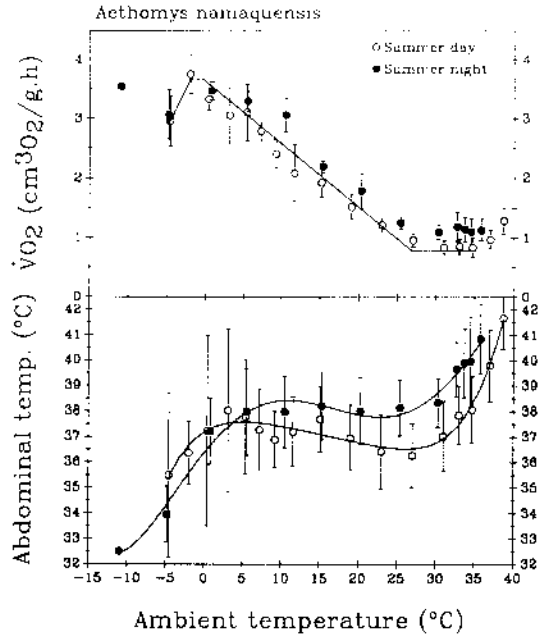

Fig. 6. Mean ± SD $\dot{V}O_2$ and T_{ab} of summer-acclimated *A. namaquensis* during the day (O) and night (●).

−15.57°C (Figs 3 and 4). Moreover, in summer animals, T_{pmr} was significantly lower at night than during the day (Fig. 3).

The day T_{pmr} of *A. namaquensis* in summer, −0.42°C, was significantly higher than that in winter, −13.53°C (Fig. 5). T_{pmr} was also significantly higher in winter during the night compared to the day (Fig. 7), but this was not the case between day and night in summer (Fig. 6).

Abdominal temperature

The rest-time T_{ab} (at T_{lc}) of summer and winter *T. paedulcus* was not significantly different, 36.12 and 36.00°C, respectively (Fig. 2), but it increased significantly to 37.59 and 37.15°C during the night in summer (Fig. 3) and winter animals (Fig. 4), respectively. Moreover, the night T_{ab} of summer animals was significantly higher than that of winter animals (Figs 3 and 4).
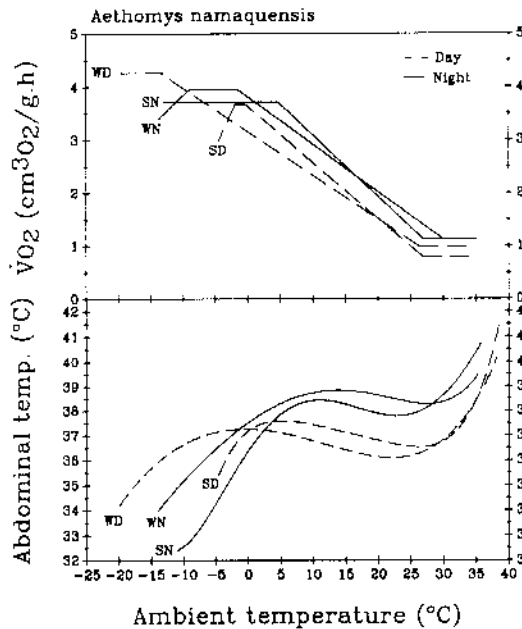

Fig. 5. $\dot{V}O_2$ and T_{ab} curves of *A. namaquensis* showing circadian and seasonal changes. See Fig. 2 legend for other details.
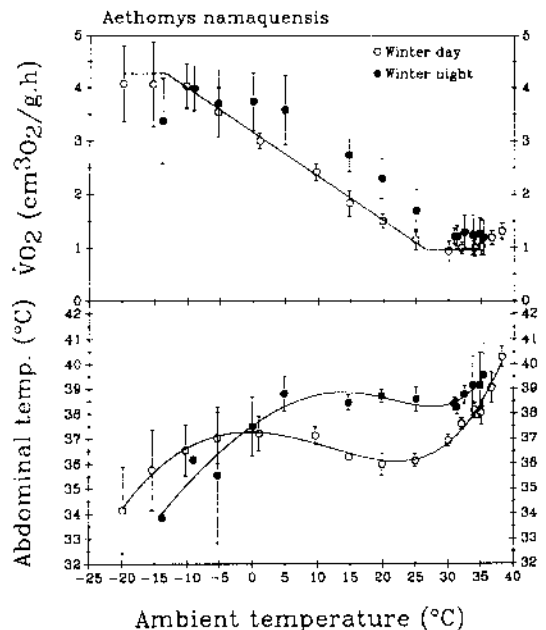

Fig. 7. Mean ± SD $\dot{V}O_2$ and T_{ab} of winter-acclimated *A. namaquensis* during the day (O) and night (●).

In all cases, T_{ab} increased below T_{lc} and reached a peak at a T_a before T_{pmr} was reached, but then decreased towards hypothermic temperatures.

The mean seasonal and circadian T_{ab} values of *A. namaquensis* were similar to those of *T. paedulcus*, i.e. no seasonal differences in the mean day and night T_{ab}s (at T_{lc}), but significant increases in the night T_{ab} from the day T_{ab} (Figs 5, 6 and 7). Moreover, T_{ab} patterns below T_{lc} showed the same sinusoidal-type patterns as those observed in *T. paedulcus*.

Body temperature cold limits

In *T. paedulcus*, the T_a at which T_{ab} fell below the T_{ab} measured at T_{lc}, i.e. T_{hypo}, showed seasonal and circadian patterns similar to those observed for T_{pmr}, except that in winter animals, T_{Tb} was significantly lower during the night, $-18.44°C$, compared with the day, $-6.10°C$ (Fig. 4), i.e. the opposite pattern to that observed between day and night in summer (Fig. 3).

A. namaquensis showed marked differences in their seasonal T_{hypo}s compared to those observed in *T. paedulcus*. Their T_{hypo} statistics were the same as their T_{pmr} statistics, but unlike *T. paedulcus*, the winter night T_{hypo} was significantly higher than that during the day (Fig. 7).

Minimal wet thermal conductance

Calculated conductances were significantly lower in winter *T. paedulcus* during the day and night, compared with those in summer. However, there was no significant change in C_{min} between the day and night in either winter or summer animals. All conductances were between 42.41 and 65.13% of predicted values. Moreover, these calculated conductances were very similar to the C_{min} values calculated from the slope of the curves of $\dot{V}O_2$ and T_a below T_{lc}.

Compared with *T. paedulcus*, the 6.0% decrease in the calculated winter day C_{min} values from summer day values was not significant in *A. namaquensis*. However, unlike *T. paedulcus*, this species significantly increased C_{min} at night in winter, but not in summer. Again, the day-time C_{min} values were considerably lower than expected, 46.58 and 42.36% in summer and winter, respectively, but were closer to expected values at night, 81.33 and 90.40% in summer and winter, respectively.

The endotherm temperature range

In *T. paedulcus*, there was no significant difference between the T_{hp} in summer (38.14°C) and winter (38.57°C). A similar comparison can not be made for the summer and winter T_{Tb} statistics, because in summer, most animals remained normothermic at T_{pmr} and data measurement did not include T_as sufficiently cold enough to reduce T_{ab} below that measured at T_{lc}. Nevertheless, the T_{tb} in winter was clearly greater than the T_{hp} in summer, which was not the case in winter, where T_{Tb} was significantly less than T_{hp}.

A. namaquensis showed large, significant increases, 40 and 42%, in the T_{hp} and T_{Tb} statistics between summer and winter, respectively.

DISCUSSION

Abdominal temperature patterns

The patterns of abdominal temperature observed in this study confirm the fact that T_{ab} is not always regulated at a constant temperature below T_{lc}, but instead, may show a sinusoidal-type pattern. These patterns can be predicted to be the thermodynamic consequence of (a) internal body conductance being at least 10-fold higher than external conductance, (b) temperature regulation with respect to T_a-dependent switching between conceptual skin and hypothalamic setpoint temperatures, and (c) the "inefficiency" of shivering-thermogenesis (SH) which causes the flattening, or a decrease in the rate of T_{ab} increase as T_a approaches T_{pmr} (Lovegrove *et al.*, 1991).

These patterns are not unique to these two species. They should be, and are often observed in other small mammals which have expected or lower-than-expected conductances and which can maintain normothermy over a wide range of T_as below T_{lc} (Lovegrove *et al.*, 1991). The patterns are not regularly observed in the literature simply because most studies do not measure $\dot{V}O_2$ and T_{ab} at T_as which are sufficiently low to induce the core–shell thermodynamic effect observed here (see Lovegrove *et al.*, 1991). The important point though, is that these patterns i.e. measuring $\dot{V}O_2$ and T_{ab} over all ambient temperatures at which the animal can maintain homeothermy, allow the calculation of useful cold limit (T_{hypo} and T_{pmr}) and ETR (T_{Tb} and T_{hp}) statistics. This study will attempt to illustrate the utility of these statistics in terms of ecophysiological interpretations of the ways in which endotherms may modify their thermoregulatory ability on a circannual and circadian basis.

Optimizing C_{min} and TRMR

Both species displayed TRMR and C_{min} statistics which were markedly lower than those predicted by the appropriate rodent allometric equations for these parameters. We will argue that these trends are consistent with predictions for rodents which face large daily fluctuations in ambient temperature, irrespective of their burrowing habits.

Firstly, since HP and conductance should both be at a minimum at $T_a = T_{lc}$, the allometric equations for rodent $TRMR = 4.98\,Mb^{-0.331}$ (Hayssen and Lacey, 1985) and that for non-primate $C_{min} = 1.53\,M_b^{-0.517}$ (Aschoff, 1982), can be substituted into the Scholander–Irving thermoregulation model:

$$RMR = C(T_b - T_a) \qquad (1)$$

and rearranged and simplified to give an equation for the expected rodent T_{lc}:

$$T_{lc} = T_{ab} - 3.25\,M_b^{0.186}. \qquad (2)$$

From equation (2) the expected summer daytime T_{lc}s of *T. paedulcus* and *A. namaquensis* can be calculated to be $T_{lc} = 28.14°C$ and $T_{lc} = 28.72°C$, respectively. Notice that these values are not too different from those actually observed in summer-acclimated animals (Table 1), despite their lower-than-expected C_{min} and TRMR values. At these predicted T_{lc}s, rodents with the same body masses as those of *T. paedulcus* and *A. namaquensis*, but with

the expected TRMRs and C_{min}s, would have similar T_{ab}s to those observed for these two species in summer (Table 1). In our animals, TRMR and C_{min} both decreased proportionally in such a way that the expected T_{lc} did not change. The pertinent question is: why are TRMR and C_{min} so low?

Let us justifiably assume that *T. paedulcus* is frequently exposed to sub-zero temperatures in its arboreal niche at night (Fig. 1), and also assume that its observed lower-than-expected C_{min} is required by the minimum T_a at which it must remain active nightly (see Lovegrove et al., 1991). We can investigate the influence of a low C_{min} on T_{ab} at T_{lc} by rearranging equation (1):

$$T_{ab} = TRMR/C_{min} + T_{lc} \qquad (3)$$

Equation (3) predicts that the T_{ab}s of *T. paedulcus* and *A. namaquensis* at T_{lc} would be 45.1 and 43.4°C, respectively, if these rodents had expected TRMRs, but also had their observed lower-than-expected conductances. Note that these are the abdominal temperatures predicted for a metabolic state in which the animal is at rest—a doubling of TRMR, such as would occur with any enforced activity state, would unrealistically elevate T_{ab}s to 61.5 and 58.6°C for *T. paedulcus* and *A. namaquensis*, respectively.

So, if these two species appear to be "stuck" with a low C_{min} required say, by the low ambient temperatures observed in winter in warm-temperate deserts at night (Fig. 1, Leistner, 1967), they are also "stuck" with the potential hyperthermic consequences thereoff. The only way to avoid grossly elevated core temperatures at, and above T_{lc}, is to reduce TRMR—which is a good explanation of the low TRMRs we report. Indeed, this interplay of lower-than-expected TRMRs and C_{min}s as means of maintaining the least variability in core temperature over a wide range of daily temperatures which include both cold and hot temperatures, i.e. maintaining high T_{Tb}s and T_{hp}s, may provide a fundamental explanation for these consistently observed patterns in desert and arboreal endotherms, irrespective of burrowing habits (see Lovegrove et al., 1991).

Circadian adjustments

Since any increase in TRMR at T_{lc} will rapidly induce hyperthermic core temperatures, we should expect warm-temperate desert rodents with low C_{min}s to increase their conductance during their circadian activity phase. However, for nocturnal species potential hyperthermia with activity onset should be less of a problem than that for diurnal species, since the onset of activity is accompanied by rapid decreases in the daily T_a towards evening (Fig. 1).

In this study *T. paedulcus* did not significantly increase their conductance at night in either winter or summer, whereas *A. namaquensis* did in winter. The thermoregulatory consequences of these two alternative physiological adjustments were that the T_{pmr} and T_{hypo} of *A. namaquensis* at night were significantly raised by ca 13°C above those possible during the day (Table 1). In other words, *A. namaquensis* became hypothermic at much higher T_as at night (Fig. 7), whereas *T. paedulcus* showed exactly the opposite pattern by decreasing T_{hypo} by 12.3°C at night (Fig. 4).

These differences highlight an irony that *A. namaquensis* has a much better thermoregulatory ability during the day than at night. In fact, the T_{pmr} (−1.52°C) of *A. namaquensis* at night was clearly higher than the absolute, minimum ambient temperatures recorded at night in the Kalahari Desert during the week of measurements (Fig. 1). This T_{pmr} therefore permits no tolerance to compensate for forced convective heat loss which must inevitably be induced by cold winds at night—an important pathway of heat loss which must be considered (see Bakken, 1976; Monteith and Mount, 1976). These day-night patterns we observe in *A. namaquensis* are therefore just the opposite from what we would expect a burrow-dwelling nocturnal rodent to display.

Burrowing behaviour and thermally-buffered refugia

The different thermoregulatory abilities of these two species at night could concern their dependency on the thermal buffering of their refugia. Although the nests of *T. paedulcus* decrease the daily ambient temperature fluctuation by ca 9°C, this buffering effect is far less than that which occurs in sealed burrows at a depth of 30 cm in the southern Kalahari Desert. Lovegrove and Knight-Eloff (1988) have shown that burrows at 30 cm in the same habitat from which the animals in this study were trapped remained remarkably constant at ca 18°C, irrespective of the time of day or the range of ambient temperature fluctuation.

Unfortunately, it is not too clear to what extent *A. namaquensis* utilize the maximum thermal buffering which is possible in burrows in the Kalahari Desert. Over their entire distributional range in southern Africa they are known to characteristically live in rock crevices (from which they get their common name), but also in holes in trees, or under "domes" of grass which they construct in the forks of trees or on the ground under low scrub bushes (Nel, 1975; Smithers, 1983; Buffenstein, 1984). The Kalahari is a vast sand desert, where *A. namaquensis* predominantly employ the latter behaviour by constructing grass domes over the entrances to their burrows which are frequently situated under low *Acacia mellifera* shrubs (Lovegrove and Knight, personal observation; Nel, 1975; Smithers, 1983). Clearly, the buffering effect of the grass domes requires quantification, but we presume that the domes must improve the thermal buffering within the burrows below.

Whatever the case, it is clear that *T. paedulcus* are considerably more limited in their ability to "escape" the extreme cold temperatures at night by entering the nest. Note from Fig. 1 that in the one week in which nest temperatures were measured, the deepnest temperature dropped to 0.6°C. This temperature and the unbuffered minimum ambient temperatures fall well within the cold limits of this species. The cold limits of *T. paedulcus* at night presumably permit an adequate heat production margin to balance wind-induced convective heat loss.

For free-ranging *A. namaquensis*, the observed seasonal interplay of reduced TRMR and C_{min} should adequately alleviate potential hyperthermia in the burrow. In mid-summer in the Kalahari, the mean temperature of sealed burrows at a depth of 30 cm remained very constant at 33.5 ± 1.3°C (Lovegrove

and Knight-Eloff, 1988). Notice that for the observed TRMR and C_{min} of *A. namaquensis*, the burrow temperature falls within the TNZ of this species in both summer (Fig. 6) and winter (Fig. 7). This confirms the earlier point that if *A. namaquensis* did not maintain a lower-than-expected TRMR, their T_bs would be markedly elevated at the observed burrow temperatures, even when at rest. In fact, the maximum diel temperatures of open burrows, which is what *A. namaquensis* seem to utilize, should be even higher than those of sealed burrows, lending further support to this argument.

The most marked influence of burrowing behaviour seems to concern the seasonal changes in the ETR statistics. In winter, *A. namaquensis* markedly increased their T_{hp} and T_{Tb} by 11.5 and 11.8°C, respectively, whereas *T. paedulcus* maintained high ETRs in both seasons. Although both species decreased their conductance in winter by 22–23%, the decrease in the T_{hypo} is more pronounced in *A. namaquensis* because this species is about half the size of *T. paedulcus*. Lovegrove *et al.* (1991) have shown that the effect of reducing C_{min} in terms of reducing the absolute cold limit of an endotherm is more marked in smaller-sized animals. Nevertheless, the observed small increases in PMR facilitated by small increases in NST_{max} must also assist in increasing the ETRs of *A. namaquensis*.

Water conservatism

It is difficult to completely assess the interelationship of our hypothesis, advocating C_{min} and TRMR optimization in terms of a habitat-dependent ETR, as an absolute alternative to the water-economy hypothesis (e.g. McNab and Morrison, 1963). Any reduction in TRMR will indeed lower core temperatures above T_{lc} (equation 1) and therefore reduce the need for evaporative cooling and evaporative water loss (Schmidt-Nielsen, 1983). Since the animal's access to food and metabolic-water (free-standing water is not common in warm-temperate deserts) may further influence the extent of TRMR reduction, the respective dietary habits of warm-temperate deserts may therefore provide a convenient approach for separating the interspecific applicability of these two hypotheses.

We may, for instance, expect seed-eaters, which rely most heavily on metabolic water, to show the lowest TRMRs and poorest heat tolerance, and folivores and omnivores (which include insects in the diet), to show intermediate TRMR adjustments and better heat tolerance.

A. namaquensis is highly omnivorous—it is a ferocious insect eater in captivity (personal observation), but also eats seeds and plant material (Nel, 1975; De Graaff, 1981). *T. paedulcus* is more vegetarian, perferring the young leaves and seed pods (not the seeds) of *Acacia* trees (Shortridge, 1934; Nel, 1975; De Graaff, 1981). Although De Graaff (1981) states that they may occasionally eat insects, unlike *A. namaquensis*, they did not show any interest in mealworms offered to them in captivity (personal observation). However, *T. paedulcus* also display a characteristic behaviour of eating the gum of *Acacia* trees (Shortridge, 1934; De Graaff, 1981). This they do by eating the gum which seeps out of hundreds of
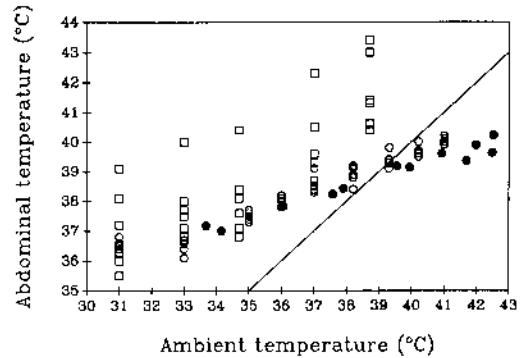
Fig. 8. Abdominal temperatures of individual *A. namaquensis* (□) and *T. paedulcus* (○) above T_{lc} measured during the day in summer-acclimated animals. Data from two female *T. paedulcus* (●) in which T_{ab} was measured while the animals were housed in a large 25 litre glass tank are included.

V-shaped grooves which they gnaw into the stems of the thinner branches of their foraging trees (Lovegrove and Knight, personal observation). These "gum-grooves" appear to be continuously maintained and may thereby provide a predictable source of plant water.

Clearly, water balance problems do not seem to pose much of a problem to *T. paedulcus* since they display a remarkable heat tolerance (Figs 2, 3 and 8) which can only be achieved via evaporative cooling. Notice that at $T_a = 41$°C, this species maintained T_{ab} at 40°C (Fig. 8). In fact, even at $T_a = 42.5$°C, two animals (dots in Fig. 8) kept T_{ab} below 40°C. As inferred by McNab and Morrison (1963), a low conductance under these circumstances also decreases the rate of heat entering the body when skin temperatures are equal to, or greater than, ambient temperatures. *A. namaquensis* on the other hand, showed far less heat tolerance. During the day in summer T_{ab} reached a mean value of 41.7°C at a T_a of 38.7°C (Figs 6 and 8). Moreover, notice the markedly lower heat tolerance at night (Fig. 7). One animal died 4 days after a night exposure to $T_a = 35.8$°C for 30 min—its T_{ab} reached 43°C. At this T_a, *T. paedulcus* maintained core temperatures which were barely higher than the lowest T_{ab}s at thermoneutrality.

Heat tolerance and its possible dependency on thermally-buffered refugia and diet can be further illustrated with a comparative study of *A. namaquensis* (C_{min} and TRMR virtually the same as in this study) and *Gerbillurus paeba* from the Namib Desert, Namibia (Buffenstein, 1984). *G. paeba* lives in plugged burrows during the day, and also had a low TRMR (52.7% of expected) and a low conductance (60.2% of expected). However, its heat tolerance was even lower than that of *A. namaquensis*. This species is not omnivorous like *A. namaquensis*—it is predominantly a seed-eater (Nel, 1975; De Graaff, 1981; Smithers, 1983).

These comparisons infer that although TRMR is indeed low in all species discussed, irrespective of their burrowing behaviour, it does not seem to be more radically decreased in those species for which we may expect water balance to pose problems. There may indeed be interspecific differences of say 5–10%

between TRMR values which are already lower-than-expected, but we would argue that these differences, even if they can be attributed to water conservation considerations, should not detract from the 30 50% reduction in expected TRMR required to avoid potential hyperthermia induced by a low C_{min}.

Much of the previous discussion has centered on the assumption that *T. paedulcus* can afford to be less water-conservative than *A. namaquensis*, possibly because of their predictable year-round reliance upon water obtained from "gum-grooves" (considered as free-standing water?). The corollary of this assumption is that water balance in rodents such as *A. namaquensis*, which may depend more on food water, will be influenced by the seasonal availability and water content of the food, and that therefore these species may be more water-conservative. By the same reasoning, water-conservatism should also be most highly developed in less-omnivorous seed-eaters.

Buffenstein *et al.* (1985) have shown that the cricetid gerbils in the Namib Desert not only had a better urine concentrating ability than various murids investigated (including *A. namaquensis* and *T. paedulus*), they also produced a crystalline allantoin precipitate in the urine which profoundly facilitated nitrogen excretion, which the murids did not. Renal performance and urine concentrating ability may therefore provide another tool for identifying the relevance in any species of either the water-economy hypothesis, or our ETR hypothesis.

CONCLUSIONS

Firstly, this study highlights the point that interspecific evaluations of the energetic adaptations of animals which differ in their behavioural exploitation of thermally-buffered refugia are made more meaningful if measurements are made (a) at all ambient temperatures over which the animal can defend endothermy, (b) during the day and night, and (c) in summer- and winter-acclimated animals. In this respect, the T_{pmr}, T_{hypo}, T_{lp} and T_{Tb} statistics proposed by Lovegrove *et al.* (1991) have proved to be useful for such interspecific comparisons.

To date, hypotheses concerning the cause of lower-than-expected TMRMs in desert rodents have converged heavily towards water-balance and "over-heating" problems. In this paper we have shown that TRMR can also be determined by the minimum conductance required to maintain endothermy over the maximum range of ambient temperatures which the animal will experience on a daily basis. In short, warm-temperate desert rodents must decrease TRMR in order to avoid elevated body temperatures at the hottest, daily ambient temperatures—a potentially heterothermic state not conducive to optimal enzyme function in endotherms.

Our hypothesis is therefore contrary to those suggesting that *A. namaquensis* " . . . compensates for reduced basal metabolic rate by having a low rate of conductance" (Buffenstein, 1984), or that " . . . this conclusion applies to desert mammals in general; if they follow the usual patterns of possessing low metabolic rates, they can maintain a normal mammalian body temperature only through a lower conductance" (Shkolnik and Schmidt-Nielsen, 1976). We have argued just the opposite, viz. that *A. namaquensis* and *T. paedulcus* have low TRMRs to compensate for a low thermal conductance.

As proposed by Lovegrove *et al.* (1991), the high energetic cost of endothermy is balanced by the animal's ability to be potentially active independent of ambient temperature constraints such that it maximizes its temporal and spatial exploitation of its habitat. The potential for activity is strongly dependent on the requirement that the body temperature of the animal be maintained within the narrowest limits possible to achieve optimal enzyme function (Hochachka and Somero, 1973), rather than on the absolute value of the regulated body temperature. Heat production is the most expensive component of an endotherm's daily energy budget, so the physiological parameter which minimises heat loss i.e. conductance, should be considered as the first, and "cheapest" line of defence of endothermy.

Concerning the influence of burrow-dwelling behaviour, we have suggested that whereas it may not have a large direct influence on TRMR and C_{min} selection, it does require warm-temperate desert rodents to markedly alter their ETRs seasonally. These seasonal ETR changes are mostly achieved with large changes in conductance—a strategy which seems to be more effectively exploited by smaller-sized, desert rodents. Although seasonal changes do occur in non-shivering thermogenesis capacity, these changes are small, certainly considerably smaller than the large seasonal changes in NST capacity observed in similar-sized cold-temperate rodents.

The distinction between the conclusion of the water-economy hypothesis and our endothermic temperature range hypothesis may, or may not, be trivial. It may be more appropriate to consider a continuum between the hypotheses based upon the animals' reliance upon thermally-buffered refugia, and its diet, water-conservatism, and heat tolerance capacity. In this respect we need to more closely define the relationship between diet/water-conservatism and heat tolerance in warm-temperate desert rodents.

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